

## SPATIAL BEHAVIOR OF EUROPEAN ROBINS DURING MIGRATORY STOPOVERS: A TELEMETRY STUDY

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**ABSTRACT.**—We studied the movement patterns of European Robins (*Erithacus rubecula*) at stopovers during spring and fall migration on the southeastern Baltic Coast, Russia. On the 1st, and sometimes the 2nd, day after arrival at a stopover site, robin movements were less aggregated than those made on subsequent days. Search/settling time varied between several hours and 2 days. During this period, migrants either occupied a defined stopover area or left the site. Stopover duration was 1 to 12 days in spring (mean = 2.4 days  $\pm$  0.31 SE) and 1 to 14 days in fall (mean = 3.4 days  $\pm$  0.50). The home-range size of European Robins on the southeastern Baltic Coast did not differ between seasons (spring: 4,320 m<sup>2</sup>  $\pm$  545,  $n$  = 15; fall: 3,562 m<sup>2</sup>  $\pm$  598,  $n$  = 15) and was similar to that at a central European site in fall (4,264 m<sup>2</sup>  $\pm$  241,  $n$  = 14). These home ranges were not defended territories. We found no relationship between the robins' spatial behavior and their fat stores on arrival, although in spring more lean than fat robins stopped for >2 days. The pattern of movements at the stopover was variable, both in birds that arrived lean and those that arrived with much more fat. Stopover duration estimates based on radio-tagging are superior to those based on capture-mark-recapture. Received 27 December 2004, accepted 23 January 2006.

Passerines spend at least 90% of their time during migration at migratory stopover sites. Stopover variables (e.g., rates of fat deposition, predation risk, habitat suitability) strongly influence migration strategies and tactics (Lindström 2003). Another important aspect of migrant stopover ecology is spatial behavior—territoriality versus broader movements, size of temporary home ranges, and sharing of home ranges versus defending them from conspecifics (Chernetsov 2003, Chernetsov and Bolshakov in press). Some migrants occupy temporary territories at stopovers (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980, 1981; Carpenter et al. 1983, 1993a, 1993b), whereas others move broadly across a given stopover area. Intraspecific variation in spatial behavior has also been reported; some individuals occupy relatively small home ranges, whereas others move over much broader areas (Aborn and Moore 1997, Delingat and Dierschke 2000). Until recently, capture-recapture analysis has been the main method for studying the pattern of movements made by passerines at stopovers (Titov 1999a, 1999b; Chernetsov and Titov 2001; Chernetsov 2002), and these

analyses suggest that—during fall (southbound) migration—European Robins (*Erithacus rubecula*) occupy defined stopover areas (DSA). Robins spend up to 2 days occupying a DSA (Titov 1999a) and, after a maximum of 2 days, either resume migration or settle in a defined home range.

An important weakness of capture-recapture analysis is that the capture probability of passerine migrants at stopovers is usually low (Chernetsov and Titov 2000) and most likely differs between groups of birds (e.g., fat versus lean birds, those refueling versus those losing weight, and new arrivals versus those occupying a DSA). Radio-tracking has been used more recently (Aborn and Moore 1997, Lajda 2001), which makes it possible to ascertain the location of a bird without having to capture it or otherwise influence its behavior.

We investigated movement patterns of radio-tagged European Robins during spring (northbound) and fall migration stopovers on the southeastern Baltic Coast, Russia. Our objectives were (1) to test the hypothesis that individuals remain within defined areas at stopover sites; (2) to estimate home-range area and settling time; and (3) to assess the impact of initial fat stores on robins' spatial behavior. Understanding patterns of spatial use by migrants within habitats, including habitats being lost or fragmented, is crucial for understanding the importance of relatively

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TABLE 1. Number and condition of European Robins radio-tagged and followed during spring (northbound) and fall (southbound) migration stopover, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia.

Season	No. tagged at stopover	No. followed from the 1st day	No. followed from the 1st to the last day	No. fat birds <sup>a</sup>	No. lean birds <sup>a</sup>
Spring					
2002	21	12	10	13	4
2003	30	30	29	16	14
Total spring	51	42	39	29	18
Fall					
2002	29	25	24	10	19
2003	36	36	35	17	19
Total fall	65	61	59	27	38

<sup>a</sup> Body mass of "lean" birds exceeded their calculated lean body mass by <1.2 g; body mass of "fat" birds exceeded their calculated lean body mass by >1.5 g.

large versus small habitat patches. Habitat use and spatial behavior of migratory landbirds have not been studied adequately, in spite of their importance as conservation issues (Petit 2000).

## METHODS

**Study site.**—We conducted our study during spring and fall, 2002–2003, at Biological Station Rybachy on Cape Rossitten on the Courish Spit, Russia (southeastern Baltic coast, 55° 09' N, 20° 51' E). Our study periods were 1 April to 4 May 2002, 13 April to 7 May 2003, 2 September to 29 October 2002, and 6 September to 8 November 2003. The overall area of the study site is 6 ha. Vegetation at the study site is a mosaic of willow (*Salix* spp.) scrub and common reed (*Phragmites communis*), and some trees, including rowan trees (*Sorbus aucuparia*), white willows (*Salix alba*), and bird cherry (*Prunus racemosa*). We mist-netted European Robins—the most commonly occurring migratory species captured at this site (Bolshakov et al. 2002)—and banded them with aluminum leg-bands (Moscow Ringing Center bands).

**Radio-tagged birds.**—We fitted 117 European Robins with radio transmitters (Table 1). To obtain unbiased estimates of stopover duration, we made every effort to tag birds just after their arrival. The rate of daily captures of small passerines, including European Robins, at our study site are highly variable (due to occurrence of migration waves), as it is at many other coastal sites (Dolnik 1975, Titov and Chernetsov 1999, Chernetsov and Titov 2000). Results of seniority analysis (i.e., cap-

ture-mark-recapture models applied backwards in time; Pradel 1996) indicate that the vast majority of European Robins initially captured on days when many new birds are banded (following a day of few captures) have just arrived (Titov and Chernetsov 1999, Chernetsov and Titov 2000).

In 2003, all birds were radio-tagged on the 1st day of a migration wave ( $n = 66$ ). In 2002, most European Robins were radio-tagged on the 1st day of a migration wave ( $n = 37$ ), while others were radio-tagged upon recapture on the 2nd or 3rd day after their initial banding ( $n = 13$ ). We assume that our estimates of stopover duration of tagged birds are unbiased.

All birds radio-tagged in fall were in their hatching year; in spring, all birds were in their 2nd calendar year. Bolshakov et al. (2003) used linear regression of body mass on wing length to calculate lean body mass of European Robins that had no visible subcutaneous fat (fat score 0, after Kaiser 1993); they made separate calculations for September, October (fall) and April (spring). Based on those calculations, all radio-tagged robins in our study were categorized as either "fat" or "lean" (Table 1); lean birds exceeded their calculated lean body mass by <1.2 g (<0.5 g in 63.4% of birds), and fat birds exceeded their calculated lean body mass by >1.5 g (>2.0 g in 93.8% of birds). If a bird was radio-tagged when recaptured rather than when it was first captured (which occurred in spring 2002), its fat score at the time of radio-tagging was used to assign it to the fat or lean group. The mass and wing length of birds at capture were re-

corded to the nearest 0.1 g and 0.5 mm, respectively.

*Telemetry protocol.*—We radio-tagged European Robins with LB-2 transmitters (Hohil Systems, Carp, Ontario, Canada). The measured life span of the transmitters was at least 10 days during spring passage and 21 days during fall migration. Transmitters were fitted as backpacks with a Rappole harness (Rappole and Tipton 1991). The weight of a transmitter with harness was 0.61 g, and the body mass of radio-tagged European Robins varied between 14.8 and 19.2 g; thus, the mass of transmitters represented 3.2–4.1% of a bird's body mass (<5% is believed to be the upper limit permissible; Caccamise and Hedin 1985, Naef-Daenzer 1993).

We used receivers with Yagi antennae from Wildlife Materials (Carbondale, Illinois) and Advanced Telemetry Systems (Isanti, Minnesota). The location of birds was estimated by biangulation and triangulation. For each individual, one location per hr was taken between the onset of daytime activity (dawn) and evening civil twilight. The number of observations per individual per day varied between 11 and 17, depending on the duration of the daylight period. Locations were plotted on a digitized map of the study area. From sunset to dawn, all birds were surveyed continuously from a stationary watch point 15 m above ground level; therefore, migratory departure time was usually detected to the nearest 1–3 min and the exact night of departure was known. Migratory departures invariably occurred during the nighttime. Generally, birds were absolutely stationary during the night (no signal change caused by movements); thus, an abrupt signal change indicated take-off. The signal could usually be received from the flying bird for some time (1–20 min), but it later disappeared. As the range of transmitter detectability did not exceed 1.5 km, signal reception from a flying bird for more than 3–4 min clearly indicated that a bird was flying in circles before choosing a direction. This behavior was very distinctive, and the probability that some other nocturnal activity was mistaken for a migratory departure was small. If a bird left the study area and occupied a home range elsewhere, the data for that bird were included only in qualitative estimates of whether or not the bird occupied a DSA. If a

bird spent the night far enough from the stationary watch point to preclude signal reception at the stationary site, we attempted to locate it every 1–2 hr until dawn. A bird was assumed to have departed if the signal could not be detected during that night.

*Data analyses.*—We tested the locations for statistical independence by using the Schoener index (Swihart and Slade 1985). The data were not formally independent (i.e., consecutive locations were aggregated with a greater-than-chance probability); nevertheless, we assumed that our data could be used for the analysis of spatial distribution. We based our assumption on the empirical rule suggested by White and Garrott (1990), which states that if enough time has elapsed between two consecutive observations for an animal to move from one end of its home range to another, the observations in question may be considered statistically independent. In our study, at least 45 min elapsed between observations, during which each individual would have had ample time to move to any point in its stopover area.

When locating birds, every effort was made to approach them as closely as possible to minimize location error. We believe that in most cases we located their positions to the nearest 5 m and, following Lajda (2001), assumed a standard deviation of 10 m. Home-range area was estimated on the basis of all locations available as 95% kernel by Animal Movement Extension in ArcView (Hooge and Eichenlaub 2000). The estimated home-range area increases with an increasing number of locations until that number reaches 40–50 (Lajda 2001); therefore, we did not estimate the home-range area of birds with <38 locations. Due to this limitation, we only estimated home-range area for the entire stopover period and for the birds that stopped for >4 days ( $n = 30$ ). To estimate the aggregation of locations from birds that were followed during shorter periods of time, we used the linearity index as applied in Animal Movement Extension of ArcView (Hooge and Eichenlaub 2000); this is the linear distance moved (i.e., the distance between the initial and final locations) divided by cumulative distance between all successive locations. The maximum value of the linearity index is 1 (i.e., if a bird is moving along a straight line). This index may be calculated for a given time interval

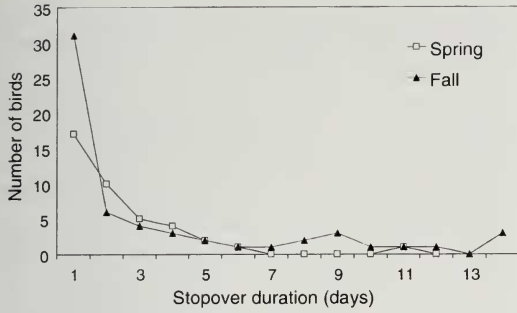


FIG. 1. Frequency distribution of stopover durations of European Robins assessed by radio tracking in spring (northbound) and fall (southbound), 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Only birds radio-tagged on the 1st day after arrival and known to depart by nocturnal flight are included. Spring: 2.4 days  $\pm$  0.31, median = 2,  $n$  = 40; fall: 3.4 days  $\pm$  0.50, median = 2,  $n$  = 59.

(e.g., the total observation period or a single day) and is a measure of area-restricted movement. The linearity index is reciprocal to the meander ratio (Williamson and Gray 1975)

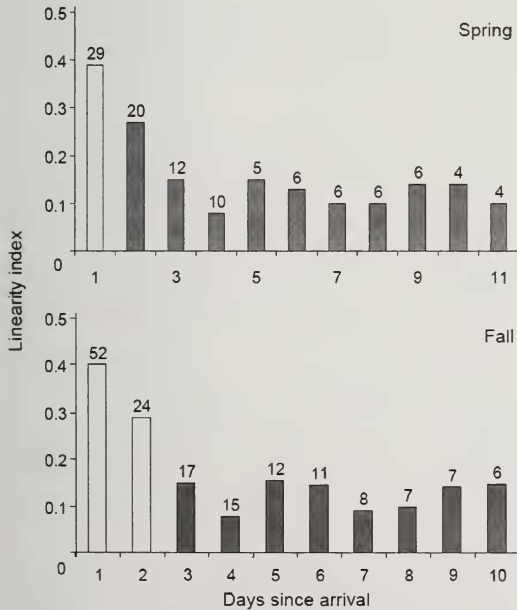


FIG. 2. Daily linearity index values of European Robins during spring (northbound) and fall (southbound) migration stopovers, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Sample sizes are shown above the histogram bars. Days with mean linearity index values significantly different from the remaining days (one-way ANOVA with post-hoc tests) are shown by open bars.

and was preferred to it due to the statistical properties of the linearity index. We used the arbitrarily selected threshold of 0.10 as an indication that a bird occupied a DSA; we assumed that birds showing linearity index values below this threshold remained in a DSA. For comparison, Aborn and Moore (1997) found that the meander ratio for Summer Tanagers (*Piranga rubra*) “settled” at stopovers on the Gulf of Mexico coast averaged 4.8, which corresponds to a linearity index of 0.21. Thus, our threshold was rather conservative.

We used  $t$ -tests to compare pairs of means when the assumption of population normality was not violated, and we used nonparametric Mann-Whitney  $U$ -tests when normality was clearly violated (e.g., distribution of stopover duration values, Fig. 1). We also used Spearman’s rank correlation when the normality assumption was violated. We used ANOVA to compare multiple samples, and we used Tukey’s honestly significant difference tests for post-hoc analyses. All tests were two-tailed; the null hypothesis was rejected if  $P < 0.05$ ; means are presented  $\pm$  SE. Data analyses were performed using SPSS version 11.0 (SPSS, Inc. 1999).

## RESULTS

### Spring Migration

*Stopover duration and establishing a DSA.*—The stopover duration of European Robins during spring migration varied from 1 to 12 days (Fig. 1). Twelve of 40 birds radio-tagged on the 1st day after arrival (30%) stopped for  $>2$  days. The mean stopover length was 2.4 days  $\pm$  0.31.

We plotted the movements of 33 birds from the 1st until the last day of stopover. We obtained at least 6, and up to 92, locations over 1–6 days from these birds. The linearity index for these birds varied from 0.008 (very aggregated locations) to 0.65 (nearly straight-line movement) and was negatively correlated with both number of locations (Spearman’s rank correlation:  $r_s = -0.69$ ,  $P < 0.001$ ) and stopover duration in days ( $r_s = -0.58$ ,  $P < 0.001$ ). The longer a bird remained at stopover, the more aggregated its locations were.

We also calculated the linearity index for each stopover day (Fig. 2). The pattern was rather obvious: during the 1st day of stopover,

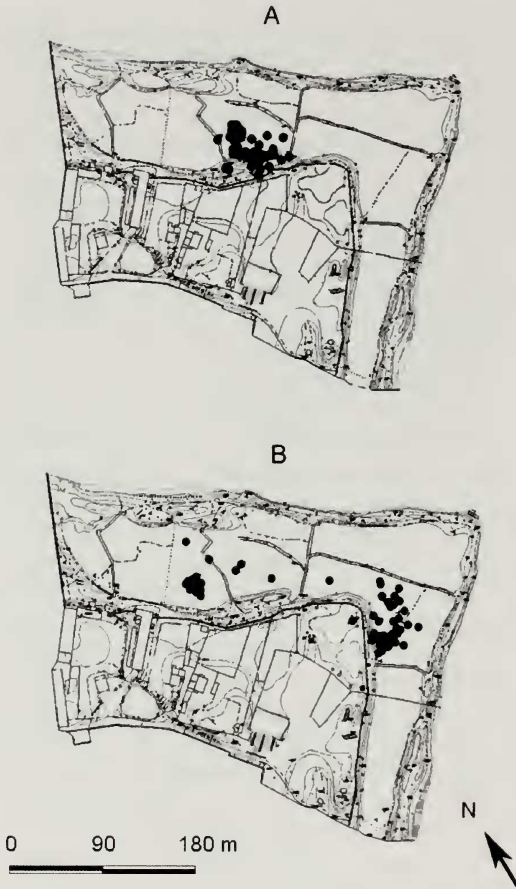


FIG. 3. Examples of the distributions of locations of two different birds during spring (northbound) and fall (southbound) migration stopovers, 2002–2003, on the Courish Spit, southeastern Baltic Coast, Russia. Each dot represents a single location. (A) All locations are in the defined stopover area (DSA). (B) Some locations are associated with the search/settling period; others are in the DSA.

robins moved broadly, and from the 2nd day on they began to remain in a more restricted area (one-way ANOVA:  $F_{10,97} = 6.85, P < 0.001$ ). The linearity index for day 1 differed from that of all other days (Tukey’s honestly significant difference test; all  $P < 0.008$ ). For movements during the first day, the linearity index did not differ between birds continuing with migration on the 1st night and those that remained for more than 1 day ( $t = 1.21, P = 0.20, n_1 = 14, n_2 = 15$ ). This means that on the 1st day of stopover, the birds behaved the same as they did on subsequent days: their movement patterns were not indicative of their subsequent decisions to remain or depart.

The movements of European Robins that remained for several days showed varying patterns. In some cases, all locations were aggregated (Fig. 3A). In others, first locations, presumably from the search/settling period, were more dispersed (Fig. 3B). We were able to estimate home-range area for 15 European Robins (where  $n \geq 38$  telemetry locations; Table 2). DSA size was negatively correlated with the number of locations ( $r = -0.54, P = 0.036$ ). Birds that stopped over for a long time (and thus yielded many location points) tended to remain within a more clearly defined area.

*Behavior of fat and lean birds.*—Of the 51 European Robins included in the analysis of spatial behavior, 18 were lean at radio-tagging (fat stores  $< 0.5$  g), 29 were fat (fat stores  $> 2$  g), and 4 had intermediate fat stores. The transmitter was removed from one lean bird, so its stopover duration was unknown. Of the remaining 17 lean birds, 10 (59%) stopped for  $> 2$  days, and mean stopover length was 3.8 days  $\pm 0.75$ . The linearity index values of all these 10 birds were  $< 0.10$ , and we assumed that they occupied a DSA. Of seven lean birds that stopped for 1–2 days, two remained with-

TABLE 2. Home-range size ( $m^2$ ) of European Robins during spring (northbound) and fall (southbound) migration stopovers on the Courish Spit (Rybachy), southeastern Baltic Coast, Russia (this study) and during fall migration in southwestern Germany (Mettnau; Lajda 2001). There was no significant difference between Rybachy and Mettnau in fall ( $t = 0.95, P = 0.35$ ) nor between seasons in Rybachy ( $t = 0.94, P = 0.38$ ).

	Range ( $m^2$ )	Mean ( $m^2$ )	Median ( $m^2$ )	SE	n	Source
Spring, Rybachy	1,932–9,215	4,320	4,091	545	15	This study
Fall, Rybachy	1,060–10,083	3,562	2,801	598	15	This study
Fall, Mettnau	1,900–7,600	4,264	4,400	421	14	Lajda (2001)

in a small defined area, three roamed broadly, and two yielded too few locations to assign their spatial behavior as either DSA owners or roamers.

Of the 29 initially fat birds, seven (24%) remained for >2 days; the mean stopover duration was 2.6 days  $\pm$  0.53. All seven birds that stopped over for >2 days occupied a DSA. Of 21 birds that departed after 1–2 days, 11 moved broadly (linearity index >0.25). The difference in stopover duration between fat and lean birds was not significant (Mann-Whitney *U*-test:  $z = 1.55$ ,  $P = 0.12$ ); however, the proportion of birds that stopped for >2 days was greater among lean birds (Yates-corrected  $\chi^2 = 4.15$ ,  $P = 0.041$ ).

Home-range area in birds that arrived fat (4,101 m<sup>2</sup>  $\pm$  493,  $n = 5$ ) and those that arrived lean (4,683 m<sup>2</sup>  $\pm$  976,  $n = 8$ ) did not differ (*t*-test,  $t = 0.44$ ,  $P = 0.67$ ); however, we could only estimate home-range area in individuals that stopped over for  $\geq 4$  days. The linearity index did not differ between birds that arrived lean and those that arrived fat on either the 1st day of stopover (fat: 0.34  $\pm$  0.039,  $n = 16$ ; lean: 0.32  $\pm$  0.059,  $n = 11$ ; median test:  $\chi^2 = 0.30$ ,  $P = 0.58$ ) or on the 2nd day (fat: 0.18  $\pm$  0.037,  $n = 11$ ; lean: 0.15  $\pm$  0.040,  $n = 6$ ; median test:  $\chi^2 = 0.03$ ,  $P = 0.86$ ). Apparently, both lean and fat birds can show various spatial patterns in the first days after arrival. We did not compare linearity indices of initially lean and initially fat birds in the subsequent (>2) days after arrival, because the chance was too high that the nutritional status of the birds had already changed.

#### Fall Migration

*Stopover duration and establishing a DSA.*—Fall stopover duration varied between 1 and 14 days (Fig. 1). Twenty-three European Robins of the 59 tracked since the 1st day of stopover remained over for >2 days. The mean stopover length was 3.4 days  $\pm$  0.50 (Fig. 1), which did not differ significantly from the duration of spring stopovers (2.4 days  $\pm$  0.31; Mann-Whitney *U*-test:  $z = 0.03$ ,  $P = 0.97$ ).

Of the birds that stopped for >2 days ( $n = 23$ ), all but one occupied a DSA. One bird that stopped for 3 days in fall 2003 covered a linear distance of  $\sim 4$  km, moving during daytime before it departed. Home-range size was

estimated for 15 individuals for which at least 39 locations were obtained per bird (Table 2). The number of locations was not significantly correlated with home-range size ( $r = -0.43$ ,  $P = 0.11$ ). The area of DSAs occupied during fall migration did not differ significantly from the area of DSAs occupied in spring (Table 2).

In fall, European Robins spent from several hr to 1.5 days moving around before settling. In one case, a European Robin that settled in a DSA on the 1st day changed its DSA on the morning of the 4th day. This individual departed by nocturnal flight after a 5-day stopover.

We tracked 42 birds from the 1st until the last day of stopover. We obtained 4–172 locations over 1–14 days from these birds. The linearity index of their movements varied from 0.003 to 0.93 and was negatively related to both number of locations (Spearman's rank correlation:  $r_s = -0.55$ ,  $P < 0.001$ ) and stopover duration in days ( $r_s = -0.56$ ,  $P < 0.001$ ). Individuals that stopped over for longer periods showed more area-restricted movement.

In fall, the linearity index differed between the days of stopover (one-way ANOVA:  $F_{9,149} = 6.69$ ,  $P < 0.001$ ). The days with linearity index values different from the others were days 1 and 2 (both different from, e.g., day 4, Tukey's honestly significant difference test:  $P < 0.001$  in both cases). Beginning with the 3rd day of stopover, there was no significant between-day variation in the linearity index (post-hoc tests; all  $P > 0.05$ ). The linearity index did not differ between the 1st and the 2nd day of stopover (Tukey's HSD test:  $P = 0.56$ ). On the 1st day, the linearity index did not differ between birds continuing migration on the next night and those that remained for more than 1 day ( $t = 0.97$ ,  $P = 0.34$ ,  $n_1 = 28$ ,  $n_2 = 27$ ).

*Behavior of fat and lean birds.*—Of 65 European Robins radio tracked in fall, 38 were lean when radio-tagged and 27 were fat (Table 1). Of the 38 lean birds, 19 (50%) stopped over for >2 days. Mean stopover duration was 4.1 days  $\pm$  0.67 (median = 2 days,  $n = 36$ ); for two birds, stopover duration was not known exactly, but was >2 days. Of the 19 lean robins that stopped over for >2 days, 18 occupied a DSA (linearity index <0.10). The

only bird with a higher linearity index (0.22), stopped for 3 days. Of the 19 lean birds that spent 1–2 days at the stopover, the movements of 10 were not very area-restricted (linearity index  $>0.25$ ). Of the 27 initially fat robins, 9 (33%) stopped for  $>2$  days, and mean stopover duration was  $3.2 \text{ days} \pm 0.69$  (median = 1 day). The difference in stopover duration between fat and lean birds was not significant (Mann-Whitney  $U$ -test:  $z = 0.74$ ,  $P = 0.43$ ). The difference in the proportion of fat and lean birds that stopped over for  $>2$  days also was not significant (Yates-corrected  $\chi^2 = 1.17$ ,  $P = 0.28$ ).

As in spring, there was no difference in the size of DSAs between initially fat ( $2,970 \text{ m}^2 \pm 518$ ,  $n = 6$ ) and initially lean ( $3,957 \text{ m}^2 \pm 939$ ,  $n = 9$ ) birds ( $t = 0.80$ ,  $P = 0.44$ ). Stopover area could be estimated only for robins that made longer stopovers ( $>4$  days), during which their nutritional status might have changed. All birds that carried large fat stores at arrival and stopped over for  $>2$  days ( $n = 9$ ) occupied a DSA. The linearity index was  $<0.10$  in all cases in which it was possible to calculate ( $n = 6$ ). Fat robins that stayed for 1–2 days ( $n = 19$ ) moved across a large area (linearity index  $>0.25$  in 10/14 cases). Five birds were tracked for too short a time to estimate their spatial status.

## DISCUSSION

Even though the maximum stopover duration assessed by radio tracking was 12 days in spring and 14 days in fall, the medians were 2 days and 1 day, respectively. In spring and in fall, 70% and 61%, respectively, of European Robins resumed migration after 1 or 2 days of stopover. Even though there was a weak tendency among lean birds to make longer stopovers, it was not statistically significant. Optimal migration theory predicts that in time-minimizing migrants, stopover duration should depend on migrant fuel status and fat-deposition rate (Alerstam and Lindström 1990). Wind direction and strength are also of paramount importance (Liechti and Bruderer 1998). Our data, like that of some other studies (e.g., Rguibi-Idrissi et al. 2003), indicate that relationships between individual stopover parameters (e.g., stopover duration and fat status) are often not as straightforward

as predicted by the necessarily simplified models.

Our telemetry study of European Robins at a migratory stopover showed that all birds that stopped over for  $>2$  days occupied a DSA. Previously, this pattern has been predicted on the basis of capture-recapture analysis (Szulc-Olech 1965, Titov 1999b); however, analysis based on recaptures is an indirect method that is strongly dependent on the recapture probabilities of the birds. Our telemetry data, which are independent of recapture probability, confirmed the hypothesis that European Robins first move around broadly, and, after 1–2 days, either settle in a DSA or resume migration. During the first 2 days after arrival, roughly one-half of the birds remained within a restricted area and one-half moved broadly (high linearity index). The latter pattern was especially typical of the 1st day after arrival. The maximum linear range of European Robin movements was  $\sim 4$  km. We suggest that these movements were associated with the search/settling period when fat-deposition rates may have been low or even negative (Titov 1999a, Chernetsov et al. 2004b). Normally, positive fat-deposition rates are not achieved until the birds settle and occupy a DSA (Titov 1999a).

Direct visual observations of radio-tagged European Robins suggested that their DSAs were not defended territories, either in spring or in fall. We frequently observed “intruders” in the core parts of occupied home ranges, quite near the owner and causing no aggression. In the vast majority of cases, Lajda (2001) observed no aggressive responses to a mounted European Robin presented to DSA owners during migration. In our study, home ranges of neighbors often overlapped, a pattern also reported by Lajda (2001). Territorial behavior in birds is known to be context-dependent (Davies and Houston 1983) and might or might not occur, depending on food distribution and availability, density of competitors, or exposure to predators. Although we did not observe territorial behavior in European Robins during migratory stopovers, we cannot rule out that, in some situations (e.g., low density of conspecifics), they might be territorial at stopovers. The DSA size used by European Robins during fall migration stopovers at Cape Rossitten did not differ between

seasons (Table 2). The size of home ranges occupied during fall stopovers on the Courish Spit did not differ from the values reported from the Mettnau peninsula in southwestern Germany (Lajda 2001). It is worth noting, however, that fall stopovers at Rybachy (3.4 days  $\pm$  0.50) were significantly shorter than those reported in southwestern Germany (6.7 days  $\pm$  1.04, Mann-Whitney *U*-test:  $z = 2.79$ ,  $P = 0.003$ ; Lajda 2001).

In our study, European Robins spent up to 2 days settling. Two days seems to be the maximum length of search/settling time, after which a robin must either establish a DSA, or leave the area. Our estimate of search/settling time, an important stopover parameter for optimal migration models (Weber and Houston 1997a, 1997b; Houston 1998; Chernetsov et al. 2004b), ranges from several hours up to 2 days. In some cases, birds that seemed to have occupied a DSA for several days would then move up to 1 km and occupy a new DSA. Even though settling within 2 days is a general rule for migrating European Robins, there may be exceptions.

We did not find a relationship between spatial behavior of European Robins and their fat stores on arrival. The only difference was that, in spring, more lean birds than fat birds stopped for >2 days. Because fat status of migrants is known to affect their foraging behavior (Loria and Moore 1990), which is closely related to spatial behavior, we had expected a difference in average stopover duration. The pattern of movements at the stopover could have been quite varied in either group. It is most likely that during stopover the fat stores of the birds changed: most individuals probably refueled, but some may have lost mass, especially during the initial phase of stopover, as observed by Rappole and Warner (1976), Moore and Kerlinger (1987), Moore and Yong (1991), and Yong and Moore (1997). European Robins that stopped over for longer periods probably gained mass, but the low number of recaptures after >3–4 days of stopover precluded us from estimating fat-deposition rates.

The proportion of birds stopping over for >2 days (30% in spring and 39% in fall) was much greater than that estimated by capture-mark-recapture models (8.4% for birds first captured during a wave of arrivals; Chernet-

sov and Titov 2000). The reason for this disagreement is probably not a delayed departure due to the effect of radio-tags (our study), but the fact that birds that leave the immediate vicinity of the release site—but remain within 500–1,000 m—are assumed in capture-mark-recapture estimates to have departed. We suggest that capture-mark-recapture estimates, and not the estimates based on telemetry data, are biased.

Occupation of DSAs, which we found in the European Robin—or occupation of territories, as reported by a number of authors for several other passerine species (Rappole and Warner 1976; Kodric-Brown and Brown 1978; Bibby and Green 1980, 1981)—is just one possible tactic employed by migrants at stopovers. Other nocturnal passerine migrants, for example, Blackcap (*Sylvia atricapilla*; Chernetsov 2002), Sedge Warbler (*Acrocephalus schoenobaenus*; Bibby and Green 1981, Chernetsov and Titov 2001), and Eurasian Reed Warbler (*A. scirpaceus*; Chernetsov and Titov 2001), occupy larger areas than do robins. In some species, authors have observed birds making broad movements, and in others they have observed birds occupying DSAs or even defending territories—e.g., the Pied Flycatcher (*Ficedula hypoleuca*; Bibby and Green 1980, Chernetsov et al. 2004a) and the Eurasian Reed Warbler (Bibby and Green 1981, Chernetsov and Titov 2001). Interspecific comparisons suggest that spatial pattern and territorial behavior of stopover migrants are probably related to the pattern of food distribution (Chernetsov and Bolshakov in press) and possibly to the density of conspecific and heterospecific competitors. European Robins forage mainly on terrestrial invertebrates, which are relatively evenly distributed across space and time (Titov 2000, Chernetsov and Titov 2003), and may occupy a DSA, at least when they make a longer stopover. Species whose prey are more unpredictable (e.g., Eurasian Reed and Sedge warblers, Chernetsov and Titov 2001; Pied Flycatchers, Chernetsov et al. 2004a), move more broadly.

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